

**Photosynthesis of *Ptelea trifoliata* L. the common hop tree (Rutaceae, rue family)
in Central Texas woodlands**

O. W. Van Auken

Department of Environmental Science and Ecology,
University of Texas at San Antonio, One UTSA Circle, San Antonio, TX 78249, USA
oscar.vanauken@utsa.edu

ABSTRACT

Measurements of photosynthetic rates were made on leaves of understory but mature *Ptelea trifoliata* L., hop tree or wafer ash plants (Rutaceae, Rue family). Plants were in *Juniperus ashei/Quercus fusiformis* (Ashe juniper/Live oak) woodlands in central Texas (98.6808W-29.6977N). Density and basal areas were low for *P. trifoliata* in the woodlands where found. External light level (PFD, photosynthetic-flux density) at midday in the open, above the canopy, was $1897 \pm 21 \mu\text{mol}/\text{m}^2/\text{s}$. Below the canopy, light level was $203 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ (mean \pm one se). Light response curves were generated using photosynthetic rates measured for leaflets on mature plants below the canopy at light levels from one to $2000 \mu\text{mol}/\text{m}^2/\text{s}$. The maximum photosynthetic rate (A_{max}) was $12.72 \pm 0.51 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ for leaflets. Dark respiration was $0.38 \pm 0.29 \mu\text{mol CO}_2/\text{m}^2/\text{s}$. Light saturation was $334 \pm 16 \mu\text{mol}/\text{m}^2/\text{s}$ or 18 % of the midday light level. The light compensation point was $10 \pm 1 \mu\text{mol}/\text{m}^2/\text{s}$ or 0.5 % of the midday high light level. Light levels below the canopy were 39 % below the light saturation point of *P. trifoliata*, which means the plants were fixing carbon at less than their A_{max} . However, for part of the day, when plants are in light gaps, gas exchange rates would be near the maximum rates measured. Based on photosynthetic rates, *Ptelea trifoliata* appears to be a potential canopy species but is more frequently in edge communities or below a woodland canopy. Published online www.phytologia.org Phytologia 103(2): 18-28 (June 21, 2021). ISSN 030319430.

KEY WORDS: CO₂ uptake, edge plants, light compensation, light levels, light saturation, photosynthetic rates, shade plants, sub canopy plants, respiration.

Below the canopy of some *Juniperus ashei/Quercus fusiformis* (Ashe juniper/Live oak) woodlands in central Texas are various shrubs, understory species, including low densities of *Ptelea trifoliata* L. (hop tree or wafer ash, Rutaceae - Rue family; Correll and Johnston 1979; Enquist 1987; Gehlbach 1988; USDA NRCS 2020). This species is one of many woody plants that have encroached into the present day woodland in this area. In central Texas and farther west this species is usually a shrub with low density but in eastern North America density can be higher and it may be a small tree (USDA NRCS 2020). Reasons for the low density and small size of these plants in the central Texas Edwards Plateau is undetermined but may be due to low or intermittent rainfall, low light below the canopy or poor competitive ability (Tilman 1985; Van Auken and McKinley 2008; Van Auken and Bush 2013; Van Auken and Smeins 2008; Van Auken 2018).

Parts of the *Ptelea trifoliata* plant have been used by Native Americans for a number of purposes (Weber and Seaman 1985). Plant leaves contain a toxin which has a strong aroma. Leaves were usually mixed with jimson weed, scorpions and other items to form a paste which was used as a poison on arrow tips for hunting large game and in warfare. Reports suggest that a slight scratch from an arrow tip so treated would insure death. Inhibitory studies and medicinal uses of various parts of this plant have also been reported (Garestier and Rideau 1972; Weber and Seaman 1985; Takaku and Setzer 2007). However, no reports of herbivory, lack of herbivory or photosynthetic rates were found.

On the eastern and southern shores of Lake Michigan there are sand dunes extending inland from the lakeshore to the mesic forests (McLeod and Murphy 1983). Populations of *P. trifoliata* have been reported from fore- and mid-sand dunes in this area. Some communities were 0.3 Ha and almost completely *P. trifoliata*. In other parts of North America and Canada this species is usually reported from the shores of lakes, streams or rivers and the understory of various forests or woodlands (USDA NCRS 2020).

Ecological conditions including photosynthetic characteristics of this species have largely been ignored; however, experimental growth was examined in sand dunes along the eastern shore of Lake Michigan (McLeod and Murphy 1983). Seed germination required cold stratification (McLeod and Murphy 1977b). There was little growth unless complete fertilizer was added to the sandy soil of the study site (McLeod and Murphy 1983). In addition, there was low transplant seedling survival (McLeod and Murphy 1977a). They serendipitously reported higher survival in shaded areas but did not pursue the importance of light levels for seedling growth. Water requirements were examined and compared with a series of western species in California (Peterson and Graves 2013). *Ptelea trifoliata* was more recently reported in Polish forests as a non-native species, but only along road cuts or forest edges with no information about light requirements (Ciosek et al. 2015).

Ptelea trifoliata is a low density and low basal area woody perennial reported from the woodland phase of some central Texas savannas (Correll and Johnston 1979; Enquist 1987; Gehlbach 1988; Leonard and Van Auken 2019; USDA NCRS 2020) and riparian forest communities (Van Auken and Ford 2017). It seems to be an understory species below the canopy in some of these communities but not in the canopy. However, reasons for its existence below the canopy are unsettled. Physiological differences among native plants in full-sun habitats compared to those found in shady, understory communities are fairly well known (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012; Keddy 2017; Poorter et al. 2019). Nevertheless, there was nothing found in the literature for *P. trifoliata* growth in sun or shade. In addition, ecological differences for growth of sun and shade plants are not always clear.

Shade species usually have low maximum photosynthetic rates (A_{max}), low light saturation, light compensation, dark respiration rates, conductance, and transpiration compared to sun adapted species (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012; Poorter et al. 2019). Most shade species are C_3 plants, characterized by a layer of horizontal leaves, and large leaf surface area, but thinner leaf blades, with more chlorophyll per mass but less per unit area than C_4 species (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012). Some species found in the understory do well in light gaps (Percy 1988; Hull 2002). *Ptelea trifoliata* seems to be an understory plant, but the reason it does well in the understory is not clear.

PURPOSES

The present study examined the light response of leaflets of *Ptelea trifoliata* in the understory of a *Juniperus ashei/Quercus fusiformis* (Ashe juniper/live oak) canopy. Gas exchange rates were measured to determine if *P. trifoliata* was a canopy or sub canopy species and to decide if its understory presence is related to its gas exchange or photosynthetic properties.

MATERIALS AND METHODS

STUDY AREA - Plants were below a *Juniperus ashei/Quercus fusiformis* canopy, on private property, near Boerne, Texas (98.6808W-29.6977N). The field site was approximately 48 km (30 miles) north of San Antonio, Texas near the southern edge of the Edwards Plateau just north of the Balcones Escarpment. Soils were Crawford Series, stony clay and shallow over hard limestone with a zero to three percent slope (USDA NCRS Accessed 2020). Surface was non-calcareous clay about 20-22 cm thick with limestone below (Mollisol over limestone bedrock, USGS NCRS 2020).

Mean annual temperature was 20°C with monthly means from 9.6°C in January to 29.4°C in July (NOAA 2018). Precipitation was 78.7 cm/yr, bimodal, with peaks in May and September (10.7 cm and 8.7 cm, respectively), with little summer rain, high evaporation, and high variability.

Vegetation in the area consisted of *Juniperus-Quercus* savanna or woodland, representative of savanna and woodlands found throughout this region, but higher in woody plant density than communities farther to the west (Van Auken et al. 1979; Van Auken et al. 1980; Smeins and Merrill 1988). Major woody species were *Juniperus ashei* (Ashe juniper) and *Quercus fusiformis* (plateau live oak). Other species included *Diospyros texana* (Texas persimmon) and *Sophora secundiflora* (mountain laurel). *Ptelea trifoliata* was present but at low density and basal area (Correll and Johnston 1979; Enquist 1987; Gehlbach 1988; Van Auken 1988; Leonard and Van Auken 2019; USDA NCRS 2020).

Interspersed in the woodlands were sparsely vegetated inter-canopy patches or gaps (Van Auken 2000). Herbaceous vegetation below the canopy was mostly *Carex planostachys* (cedar sedge, Wayne and Van Auken 2008). The gap species included *Aristida longiseta* (red threeawn), *Bouteloua curtipendula* (side-oats grama), *Bothriochloa laguroides* ssp. *torreyana* (silver bluestem), *B. ischaemum* var. *songarica* (King Ranch bluestem), various other C₄ grasses, and a variety of herbaceous annuals (Correll and Johnston 1979; Enquist 1987). Light levels and soil temperatures were higher in the gaps than the associated woodland (Wayne and Van Auken 2004; Boeck and Van Auken 2017).

GAS EXCHANGE - Gas exchange and light levels were measured with a **Li-Cor** 6400 portable photosynthetic meter. Photosynthetic-flux density (**PFD**) was the fixed variable. Plants were fully leafed out in April 2020 when leaflets were measured, within \pm three hours of solar noon. Gas flow rate was 400 $\mu\text{mol/s}$ and CO₂ concentration was 400 $\mu\text{mol/mol}$ with **PFDs** as follows: 1, 5, 10, 25, 50, 75, 100, 200, 400, 600, 800, 1000, 1200, 1600, 1800 and 2000 $\mu\text{mol/m}^2/\text{s}$. The leaflets measured covered the entire chamber surface (Van Auken et al. 2020).

Plants growing below a *Juniperus ashei/Quercus fusiformis* canopy were selected and five fully expanded leaflets were measured. Plants in the shaded understory were at light levels of 203 ± 28 $\mu\text{mol/m}^2/\text{s}$ (mean \pm se) with a range from 29 to 335 $\mu\text{mol/m}^2/\text{s}$. Canopy leaves were at 1897 ± 21 $\mu\text{mol/m}^2/\text{s}$.

Replicate gas exchange values for each parameter were measured and then means were determined. Calculated values were for the following parameters: maximum photosynthetic rate ($A_{\text{max}} = \mu\text{mol CO}_2/\text{m}^2/\text{s}$), photosynthetic-flux density **PFD** at A_{max} ($\mu\text{mol/m}^2/\text{s}$), transpiration ($\mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$), conductance ($\text{mmol H}_2\text{O}/\text{m}^2/\text{s}$), light saturation point ($\mu\text{mol/m}^2/\text{s}$), dark respiration ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$), light compensation point ($\mu\text{mol/m}^2/\text{s}$), and the quantum yield efficiency ($\mu\text{mol CO}_2/\mu\text{mol quanta}$). Data for each replicate leaflet was fit to the model of Prioul and Chartier (Prioul and Chartier 1977) using the PC software package Photosyn Assistant (Dundee Scientific, Dundee, Scotland).

The A_{max} was the highest net photosynthetic rate. Light saturating photosynthesis depicted the **PFD** when the slope of the initial rate line reached the A_{max} . Dark respiration was the gas exchange rate at a **PFD** of 0 $\mu\text{mol/m}^2/\text{s}$ (y-intercept of the line for the initial rate). The light compensation point was calculated as the **PFD** when the photosynthetic rate was 0 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (x-intercept of the line for the initial rate). The quantum yield efficiency was calculated using the dark value and increasing **PFDs** until the regression coefficient of the slope decreased.

Light response curves were generated for each leaflet. Assumptions for parametric statistics were met (Shapiro Wilk test for normal distribution and O'Brien .5 test for equal variance [Sall et al. 2017] variance was high but not significantly different). A one-way ANOVA was completed for several variables followed by the Tukey Kramer HSD to determine if differences occurred at various **PDF** levels (Sall et al. 2017). An alpha value of 0.05 was used throughout.

RESULTS

A mean photosynthetic light response curve was created for leaflets of *Ptelea trifoliata* (Figure 1). Plants were found in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of $203 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$. The curve produced is a 2nd order positive polynomial that reached a steady state at higher light levels. The mean photosynthetic rate for the leaflets of *P. trifoliata* was $5.43 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ ranging from -1.012 at the lowest light level measured (dark respiration) to $10.72 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ at the highest light level with 16 light levels measured. There were significant differences in photosynthetic rates between several of the light levels (one-way ANOVA $p = < 0.0001$, followed by the Tukey Kramer HSD multiple range test $p = < 0.05$, Figure 1, Table 1).

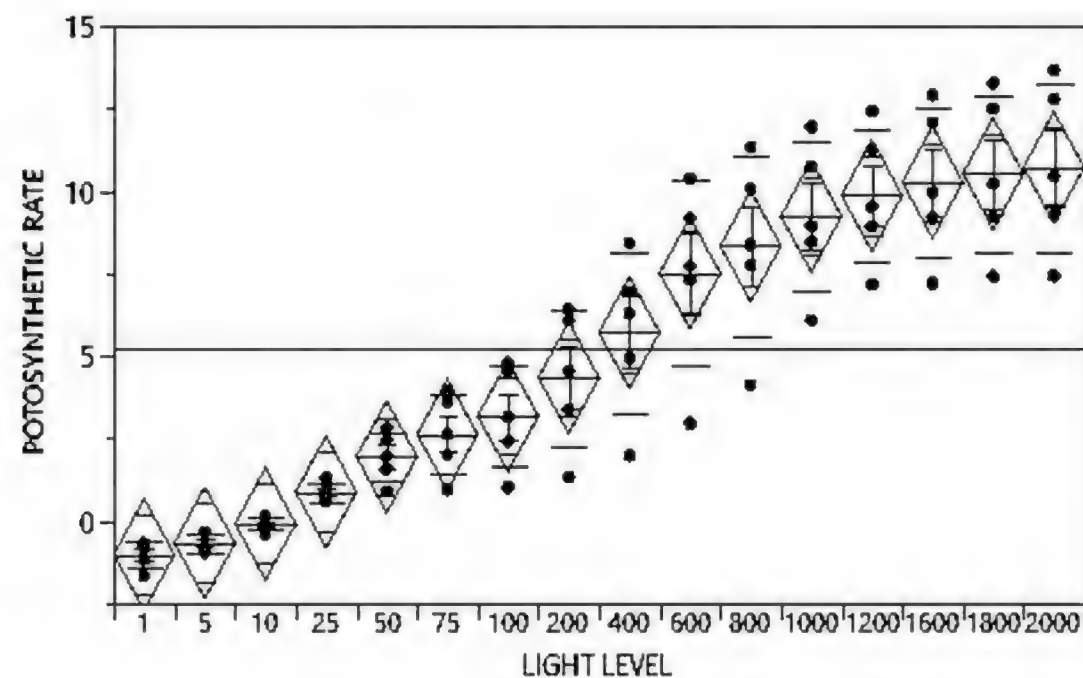


Figure 1. Mean photosynthetic rates for *Ptelea trifoliata* measured at light levels from $1 \mu\text{mol}/\text{m}^2/\text{s}$ to $2000 \mu\text{mol}/\text{m}^2/\text{s}$. Each black dot is a replicate at a given light level. A diamond includes the sample mean (middle horizontal bar and each apex is ± 1 confidence interval). The Range of photosynthetic rates was from -1.012 to $10.72 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ (the lowest measurements were negative or dark respiration rates). Standard error at $2000 \mu\text{mol}/\text{m}^2/\text{s}$ was $2.01 \mu\text{mol CO}_2/\text{m}^2/\text{s}$. Plot is best represented by a 2nd order polynomial function ($y = -2\text{E}-07x^2 + 0.001x + 0.64$) with a high R^2 value (0.97). Note plot is not linear with lower values emphasized. The p value for the one-way ANOVA was < 0.0001 . Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of $203 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ (mean \pm se). Measurements were made on April 16, 2020.

Because of high variance (Figure 1), it is difficult to see significant differences in photosynthetic rates at different light levels. Consequently, table 1 must be used (connecting letters table). Light levels are on the left and mean photosynthetic rates are on the right. If the letters in a row are the same, there is no significant difference between the photosynthetic rates between the light levels. For example, letters in the table (second row from the left) show that there were no significant differences in photosynthetic rates between light levels of 600 and $2000 \mu\text{mol}/\text{m}^2/\text{s}$ (all "A's"). In addition, there were no significant differences in carbon uptake rates between light levels of zero and $75 \mu\text{mol}/\text{m}^2/\text{s}$ (only "F's"). Nevertheless, these low light levels were significantly different from the photosynthetic rates measured between 600 and $2000 \mu\text{mol}/\text{m}^2/\text{s}$. Photosynthetic rates between light levels of 75 and $600 \mu\text{mol}/\text{m}^2/\text{s}$ were intermediate but for the most part not significantly different from the high or low photosynthetic rates (note the "B" and "C's" as well as the "D" and "E's").

Table 1. Connecting letters table for each mean photosynthetic rate in figure 1 at each measured light level from $1 \mu\text{mol}/\text{m}^2/\text{s}$ to $2000 \mu\text{mol}/\text{m}^2/\text{s}$ (left column). Range of photosynthetic rates for *Ptelea trifoliata* was from -1.012 to $10.72 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ (negative measurements were dark respiration rates). The p value for the one-way ANOVA was < 0.0001 . Light levels followed by the same letter are not significantly different ($p < 0.05$ Tukey Kramer HSD). Levels not connected by same letter are significantly different.

Connecting Letters Report		
Light Level		Mean
2000	A	10.72
1800	A	10.53
1600	A	10.27
1200	A B	9.86
1000	A B	9.24
800	A B C	8.34
600	A B C	7.51
400	B C D	5.72
200	C D E	4.35
100	D E F	3.18
75	D E F	2.63
50	D E F	1.95
25	E F	0.88
10	F	-0.08
5	F	-0.66
1	F	-1.01

Transpiration changed as a function of light level being highest on the upper part of the light response curve (Figure 2). Mean stomatal conductance and transpiration followed a similar trend with high values at high light levels, decreasing as light levels decrease (stomatal conductance not shown).

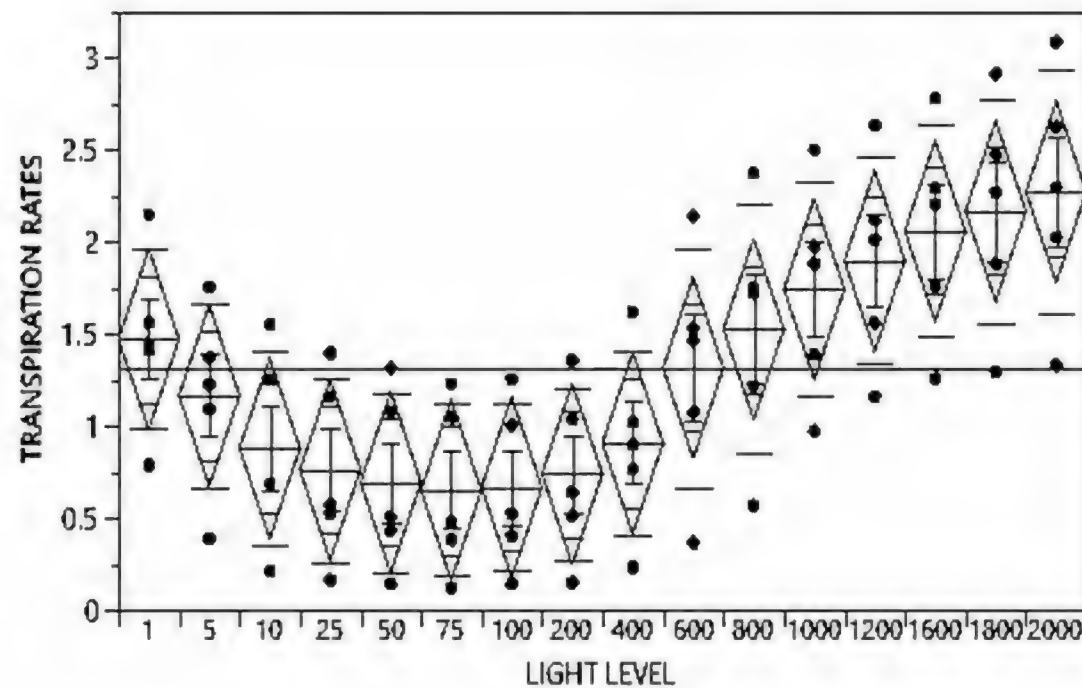


Figure 2. Mean transpiration rates for *Ptelea trifoliata* measured at light levels from 1 $\mu\text{mol}/\text{m}^2/\text{s}$ to 2000 $\mu\text{mol}/\text{m}^2/\text{s}$. A diamond includes the sample mean (middle horizontal bar and each apex is ± 1 confidence interval). Each black dot is a replicate at a given light level. Range was from 0.651 to 2.274 $\text{molH}_2\text{O m}^2/\text{s}$. Standard error at 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ was 0.145 $\text{mol H}_2\text{O}/\text{m}^2/\text{s}$. Plot is best represented by a 2nd order polynomial function ($y = -2\text{E}-07x^2 + 0.001x + 0.64$) with a high R^2 value (0.97). Note plot is not linear with lower values emphasized. The p value for the one-way ANOVA was <0.0001 . Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of $203 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ (mean \pm se). Measurements were made on April 16, 2020.

There were significant differences in transpiration rates between several of the light levels (one-way ANOVA $p = < 0.0001$, followed by the Tukey Kramer HSD multiple range test $p = < 0.05$, Figure 2). The highest mean transpiration measured was 2.274 $\mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$ at a PDF of 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ with a mean overall value of $1.308 \pm 0.226 \mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$ (Table 2). Measured transpiration rates (E_{leaf}) vs. light levels were between approximately 10 and 20 times higher than stomatal conductance. Again, because of high variance (Figure 2) it is difficult to see significant differences in transpiration rates at different light levels. Consequently, table 2 must be used (connecting letters table). Transpiration rates between light levels of 1600 and 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ were not significantly different but were significantly different than values between 25 and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (Table 2). Values between 400 and 1200 $\mu\text{mol}/\text{m}^2/\text{s}$ were not significantly different from each other or the higher values.

Table 2. Connecting letters table for each mean transpiration rate in figure 2 at each measured light levels from 1 $\mu\text{mol}/\text{m}^2/\text{s}$ to 2000 $\mu\text{mol}/\text{m}^2/\text{s}$. Range was from 0.651 to 2.274 $\text{mol H}_2\text{O m}^2/\text{s}$ Standard error at 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ was 0.145 $\text{mol H}_2\text{O}/\text{m}^2/\text{s}$. The p value for the one-way ANOVA was <0.0001 . Light levels followed by the same letter are not significantly different ($p < 0.05$ Tukey Kramer HSD). Levels not connected by same letter are significantly different.

Connecting Letters Report		
Light Level		Mean
2000	A	2.274
1800	A	2.169
1600	A B	2.061
1200	A B C	1.899
1000	A B C D	1.745
800	A B C D	1.528
1	A B C D	1.472
600	A B C D	1.316
5	A B C D	1.166
400	B C D	0.907
10	B C D	0.880
25	C D	0.762
200	C D	0.740
50	C D	0.695
100	C D	0.668
75	D	0.651

A_{max} (mean maximum estimated photosynthetic rate) for leaflets of *P. trifoliata* was 12.72 ± 0.51 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Table 3, calculated from Prioul and Chartier 1977). Quantum yield efficiency (Φ) or initial slope (IS) for leaflets of *P. trifoliata* was 0.039 ± 0.006 $\mu\text{mol CO}_2/\mu\text{mol quanta}$ (Table 3). Light compensation (L_{cp}) was 10 ± 1 $\mu\text{mol}/\text{m}^2/\text{s}$, light saturation (L_{sat}) was 334 ± 42 $\mu\text{mol}/\text{m}^2/\text{s}$ and dark respiration (R_d) was 0.38 ± 0.29 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Table 3). The highest conductance (g_{leaf}) measured was 0.218 $\mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$ at a PDF of 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ with a mean overall value of 0.083 ± 0.014 $\mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$ (Table 3).

Table 3. Comparison of mean \pm one se for the maximum net photosynthetic rates (A_{max}), light level (PDF) at the A_{max} , and other photosynthetic parameters for *Ptelea trifoliata*, and *Phaseolus texensis* (a shade plant) and two known sun plants (one herbaceous and one woody) from central Texas are presented. Leaflets were growing on *P. trifoliata* plants found in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of 203 ± 111 $\mu\text{mol}/\text{m}^2/\text{s}$.

Parameter	<i>Ptelea trifoliata</i> *	<i>Phaseolus texensis</i> **	<i>Heliotropium tenellium</i> ***	<i>Juniperus ashei</i> ****
A_{max} -max. photo. rate	12.72 ± 0.51	5.99 ± 0.17	34.96 ± 4.43	9.42 ± 0.85
Light Level at A_{max}	2000	1000	2000	2000
L_{sat} - Light saturation	334 ± 42	155 ± 19	591 ± 122	353 ± 38
L_{cp} - Light comp. point	10 ± 1	0.10 ± 0.00	38 ± 3	23 ± 20
R_d - Dark respiration	0.38 ± 0.29	0.24 ± 0.14	2.63 ± 0.38	1.8 ± 0.2
IS - Initial slope	0.039 ± 0.006	0.038 ± 0.007	0.07 ± 0.01	0.046 ± 0.026
g_{leaf} - Stomatal cond.	0.083 ± 0.014	0.068 ± 0.080	0.44 ± 0.08	0.095 ± 0.014
E_{leaf} -Transpiration	1.308 ± 0.226	0.705 ± 0.950		

*This study **Van Auken et al. (2020) ***Boeck and Van Auken (2017) ****Grunstra (2008)

DISCUSSION

Many characteristics of plants are determined by light levels present where a plant is growing (Boardman 1977; Holt 1995; Keddy 2017; Poorter et al. 2019). Wavelength, intensity, and duration are potentially important light characteristics that may determine leaf characteristics (Holt 1995; Poorter et al. 2019). In the present study, sub canopy leaves of *Ptelea trifoliata* were examined to survey photosynthetic variables from mature plants found in shade below a *Juniperus ashei* canopy. No canopy *P. trifoliata* plants were found in these central Texas woodlands. Exposing sub canopy leaves to high light levels increased carbon uptake values to levels equivalent to associated trees in this area (*J. ashei*, Table 3). This was consistent with observations that *P. trifoliata* is a mid to late successional woodland or forest species and is similar to what has been shown for some other species (Bazzaz and Carlson 1982; Hull 2002; Grunstra 2011; Van Auken and Bush 2013).

Gas exchange rates of a number of species of trees, shrubs and herbaceous C_3 and C_4 species from central Texas glades, woodlands, and forests have been examined (Table 3; Van Auken and Bush 2013, 2015; Van Auken 2018; Van Auken et al. 2020). *Ptelea trifoliata* A_{max} rates were higher than *Juniperus ashei* A_{max} rates which is currently the major canopy species in this area (Table 3; Grunstra 2011). This suggests that *P. trifoliata* could be a canopy species in these woodland communities in the future. Three herbaceous species had higher A_{max} rates than *P. trifoliata* (Van Auken and Bush 2011; Boeck and Van Auken 2017) as did five C_4 grasses measured in full sun (Wayne and Van Auken 2008, 2011) while three herbaceous C_3 shade adapted species had lower A_{max} rates (Van Auken 2018). The sun species could overgrow *P. trifoliata* juveniles in full sun and the other woody plants would probably overgrow *P. trifoliata* juveniles in shade because of higher light compensation points (Table 1, Van Auken and Taylor 2020).

It seems that *P. trifoliata* juveniles growing in shade have low photosynthetic rates when growing in shade equivalent to most sub canopy species, but in light gaps rates would increase to rates equivalent to the canopy leaves in full sun. This would be higher than most understory or sub-canopy plants allowing them to exceed growth of their neighbors (Hull 2002; Sefcik et al. 2006; Kim et al. 2015). However, this does not seem to happen. In eastern North American forests, *P. trifoliata* is a small, understory tree that does not seem to reach the canopy (USDA NCRS 2020). No information on the photosynthetic rates and other physiological leaf parameters of *P. trifoliata* were identified in the literature. I assume *P. trifoliata* is at least moderately shade tolerant, because of reports of its distribution in woodlands and forests communities (USDA NCRS 2020) and results reported here. Reasons for its ability to persist in these communities have not been explained, but potential slow growth of *P. trifoliata* suggests shade tolerance, as photosynthetic parameters are tied to growth rates (Coley et al. 1985; Larcher 2003; Sefcik 2006; Keddy 2017; Van Auken et al. 2017; Poorter et al. 2019).

Factors known to drive succession are temporal differences in resource availability especially soil resources and light levels (Tilman 1985; Van Auken and Bush 2013). Early successional species are shade intolerant requiring high light levels and low levels of soil nitrogen with late successional species being the reverse (Boardman 1977; Tilman 1985; Valladares and Niinemets 2008; Van Auken and Bush 2013). As increasing canopy shade decreases available light at the surface, shade tolerant and higher soil nitrogen requiring species become more common (Tilman 1985; Bush and Van Auken 1986; Van Auken and Bush 2013). *Ptelea trifoliata* juveniles may be able to increase their photosynthetic rates to take advantage of sunflecks and variable levels of soil nitrogen, but no data were found to demonstrate this (Percy 1988; Hull 2002; Kim et al. 2015) and no papers were found concerning their competitive abilities in sun or shade.

Early successional species exhibit higher rates of photosynthesis, transpiration, and conductance than late successional species while late successional or climax community species are more likely to be shade tolerant and reach their light saturation points at much lower light levels (Horn 1975; Wayne and Van Auken 2008; Van Auken and Bush 2011, 2015; Nelson Dickerson and Van Auken 2017). In the current study, sub canopy leaves had low gas exchange rates when measured at low light levels, but when light levels were increased, gas exchange rates increased until they approach the A_{max} of the overstory leaves. Early succession sites also have greater variability in abiotic conditions, and early successional plants frequently have greater plasticity in their adaptive responses than late successional species (Horn 1975; Hull 2002; Van Auken and Bush 2011, 2015).

Transpiration rates (E) and stomatal conductance (g_s) rates for *P. trifoliata* were light dependent with higher rates at higher levels of light. Dry surface soils suggesting low soil water levels did not seem to be a problem as indicated for other species, but this was not tested (Boardman 1977; Bsoul et al. 2007). Transpiration and stomatal conductance rates seemed to be consistent with values for shade tolerant species (Horn 1975; Boardman 1977; Bazzaz and Carlson 1982; Tilman 1985; Hull 2002; Valladares and Niinemets 2008; Van Auken and Bush 2013).

Plants with low photosynthetic rates may experience lower growth potential below the canopy and have difficulty getting through the canopy without a disturbance or mortality of canopy plants that could create a light gap or patch (McKinley and Van Auken 2005; Kain et al. 2011.). When this lowered growth potential is combined with possible browsing pressure on the target species, in this case *P. trifoliata*, the effect of light level can be stronger (Van Auken and Bush 2009; Leonard and Van Auken 2013).

Community composition in central Texas woodlands seems affected by complex interaction of photosynthetic capacities and other factors including competition and preferential feeding of large herbivores. Many species in these central Texas communities that grow in high light cannot grow in deep shade below a closed canopy and the reverse seems to be true as well (McKinley and Van Auken 2005;

Wayne and Van Auken 2008; Furuya and Van Auken 2010; Grunstra 2011; Grunstra and Van Auken 2015).

Ptelea trifoliata plants in central Texas are relatively rare and appear to be outliers (Gehlbach 1988; Leonard and Van Auken 2019; USDA NCRS 2020). Understanding that they are understory, sub canopy species or shade tolerant species was unknown until the present study. Management of these populations in the past has mostly been haphazard at best and dependent on the whims of owners of properties where this species occurs (Carpenter and Brandimarte 2014). Sensitivity to herbivory for many species in this area is not well demonstrated (Leonard and Van Auken 2013, 2019; Van Auken and Taylor 2020) nor is competitive ability. What will happen to these species and populations in the future is uncertain and difficult to predict. With disruption of reproduction by herbivory, habitat loss or other factors, many species in central Texas will probably become extinct. What is the timeline of the potential expatriation of these isolated native species? This is uncertain at this time. It is hard to say because many individuals of these woody species can live for hundreds of years. In addition, death rates of adults are unknown and the rate of recruitment of juveniles into these populations is unknown.

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